SEASONAL ABUNDANCE, DISTRIBUTION, HOSTS AND TAXONOMIC PLACEMENT OF *DIPTEROPHAGUS DACI* DREW & ALLWOOD (STREPSIPTERA: DIPTEROPHAGIDAE)

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Abstract

Nineteen species of dacine fruit flies are recorded as hosts of *Dipterophagus daci* Drew and Allwood, a strepsipteran parasite which has been reared only from Tephritidae. Aspects of the ecology of *D. daci* in northern Australia, in relation to the seasonal abundance of its two most abundant hosts, *Bactrocera aquilonis* (May) and *B. tenuifascia* (May), are reported. Monthly captures of the two hosts over a 12 month period indicated that their populations increased with the onset of higher temperatures, moisture levels and availability of host fruits. Numbers of *D. daci* peaked about one month after *B. aquilonis* and two months after *B. tenuifascia* and evidence indicated that the seasonal activity of *D. daci* was dependent upon the availability of its host and rainfall. Higher levels of parasitism occurred in *B. aquilonis* than in *B. tenuifascia* and rapid increase in host populations was probably one significant factor in the prevention of the parasite from causing a high level of parasitism during the period of high fruit fly population. The fruit flies and their parasites were more abundant in wet than dry habitats. *D. daci* is recorded for the first time from the Solomon Islands. The family Dipterophagidae is reinstated.

Introduction

Most species of Strepsiptera occur in the Palaeotropical region of the world which incorporates the tropics and subtropics (Kinzelbach 1978). Little is known about the biology and ecology of these insects and no information has been reported on the seasonal abundance of species or levels of parasitism achieved in nature. The most comprehensive biological study was on a strepsipterous parasite of *Antestia* spp. (Pentatomidae) by Kirkpatrick (1937). Brief accounts of general biology and life histories have been reported by Perkins (1905), Ogloblin (1939), Bohart (1941) and Riek (1970), while Raatikainen and Heikinheimo (1974) studied the flying times of strepsipteran males at different latitudes in Finland.

Fruit flies (Tephritidae: Dacinae) are endemic to northern and eastern Australia. Considerable research has been undertaken on the ecology of Dacinae in endemic tropical and subtropical rainforest habitats and in cultivated orchards (Fitt 1981, Drew and Hooper 1983, Fletcher 1987). The influence of hymenopterous parasites and various predators was investigated by Drew (1987) in rainforest habitats. Major reductions in fly populations were due to fruit-eating vertebrates and hymenopterous parasites had only a minor effect.

Dipterophagus daci Drew and Allwood is unique in being the only strepsipteran species so far described which is a parasite of Diptera. It is most abundant in the Northern Territory where it parasitises a number of fruit fly species. Because of the economic importance of fruit flies to Australia, including some of the hosts of *D. daci*, data have been collected on host

Fig. 1. Location of trapping sites and meteorological stations used in this study.

records, seasonal abundance and geographic distribution of the parasite in its endemic habitats. Percent parasitism levels have been calculated also.

Taxonomic note

The family Dipterophagidae was established for *D. daci* based on a combination of male, female and first stage larval characters (Drew and Allwood 1985). Kathirithamby (1989) treated it as a subfamily of Halictophagidae on the basis of a number of characters that *D. daci* and known halictophagids have in common. However, other families of Strepsiptera also possess some of these characters and families such as Bohartillidae were separated on the basis of one of these characters (number of antennal segments).

Kathirithamby (1989, 1992) noted that most species placed in the Halictophagidae are parasites of Hemiptera and that all (except *D. daci*) had males with seven antennal segments and lateral flabella on more than one segment (except in the Tridactylophaginae which has one lateral flabellum and parasitises Orthoptera) and females with abdominal segments 1-5 with one genital aperture each and the cephalothorax flattened. A measurement of the 7th antennal segment of *D. daci* was given (Kathirithamby 1989, p. 78) but this species has only six such segments. Also it was stated that the female of *D. daci* possessed genital pores on abdominal segments 4-6 (Kathirithamby 1989, pp 76, 78) or 3-6 (Kathirithamby 1992, p. 166). However, this species has genital pores on abdominal sterna 3-5 (Drew and Allwood 1985).

The following combination of characters is unique to *D. daci*: male with six antennal segments and a lateral flabellum on segment 3 only; female with a bell-shaped (rounded) cephalothorax and genital openings on abdominal sterna 3-5. These characters, plus the host, render it very distinct from all true halictophagids and the family Dipterophagidae is reinstated.
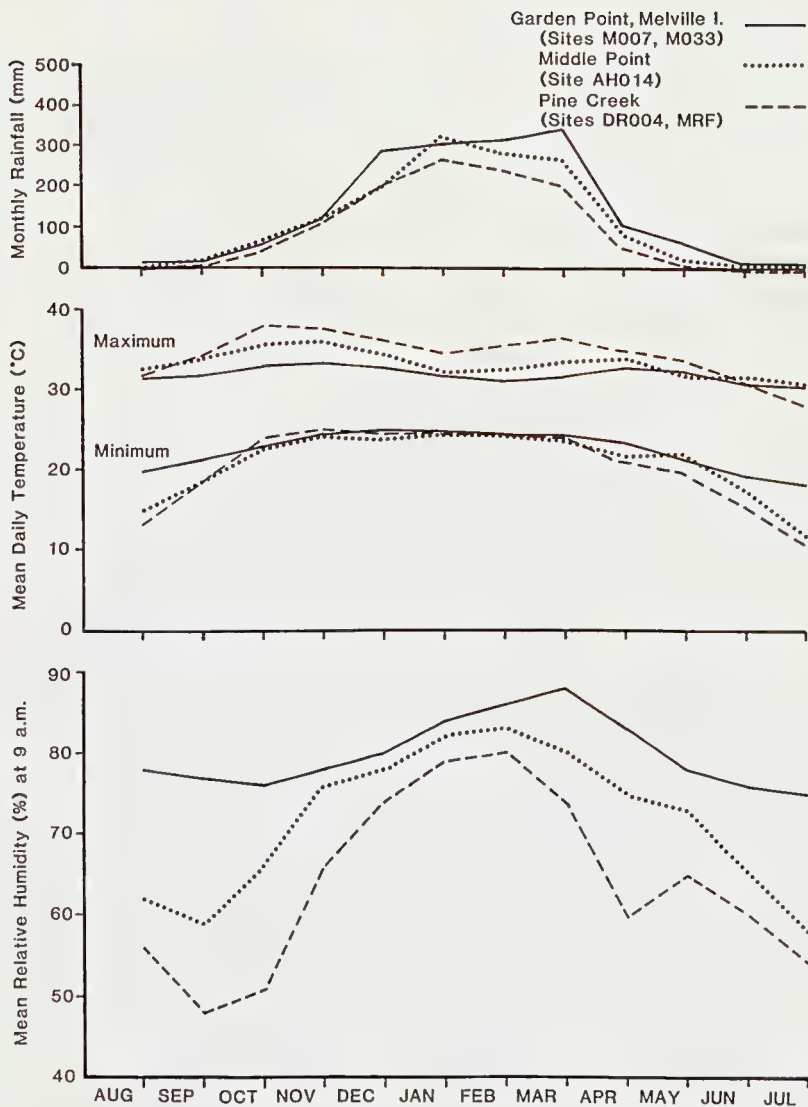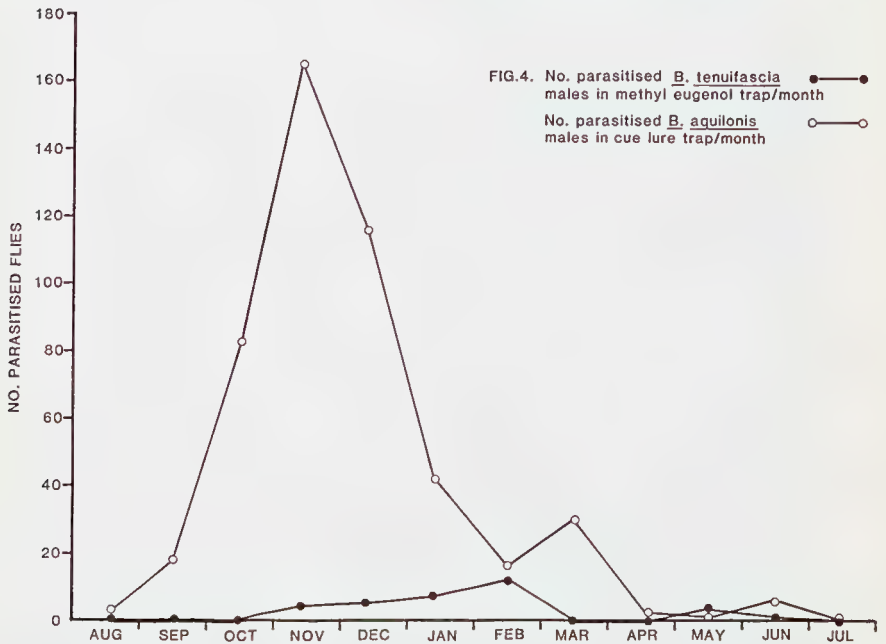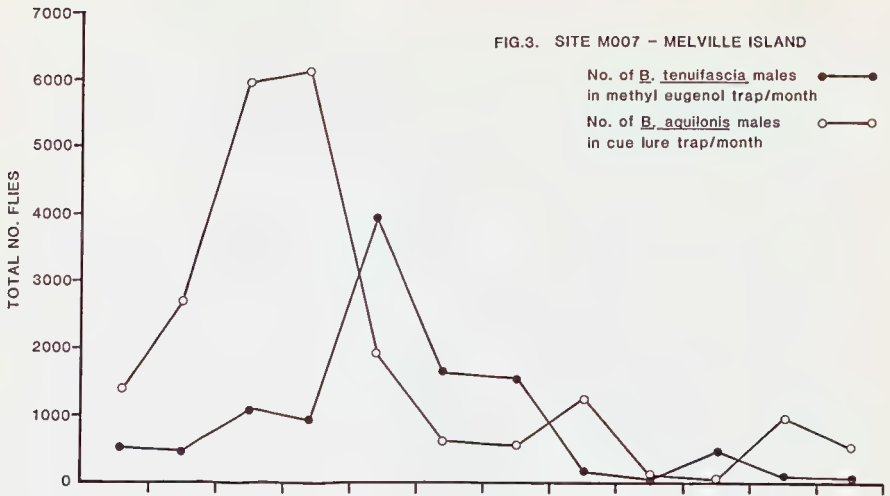
Fig. 2. Meteorological data (monthly rainfall, mean maximum and minimum daily temperatures and mean relative humidities at 9 am) at weather stations that represent trapping sites.

FIG.3.   SITE M007 — MELVILLE ISLAND

No. of B. tenuifascia males
in methyl eugenol trap/month

No. of B. aquilonis males
in cue lure trap/month

FIG.4.   No. parasitised B. tenuifascia
males in methyl eugenol trap/month

No. parasitised B. aquilonis
males in cue lure trap/month

TOTAL NO. FLIES

NO. PARASITISED FLIES

AUG   SEP   OCT   NOV   DEC   JAN   FEB   MAR   APR   MAY   JUN   JUL

Figs. 3 and 4. (3). Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month at site M007 on Melville Island; (4). Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month parasitised by *Dipterophagus daci* at site M007 on Melville Island.
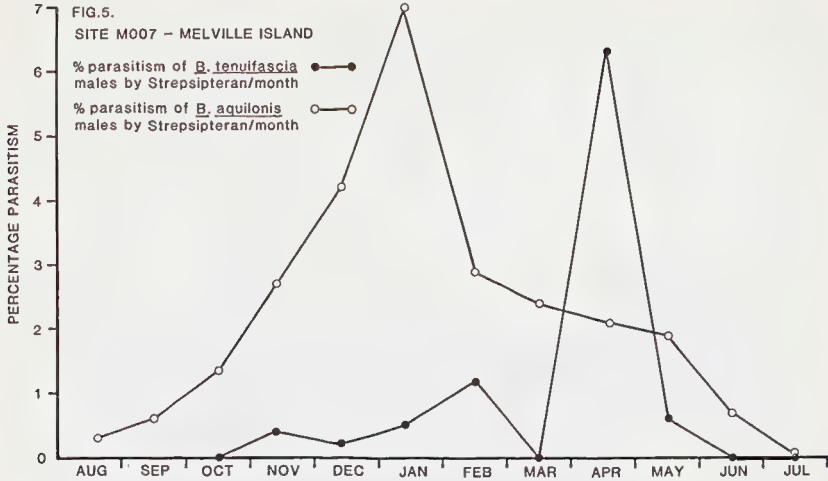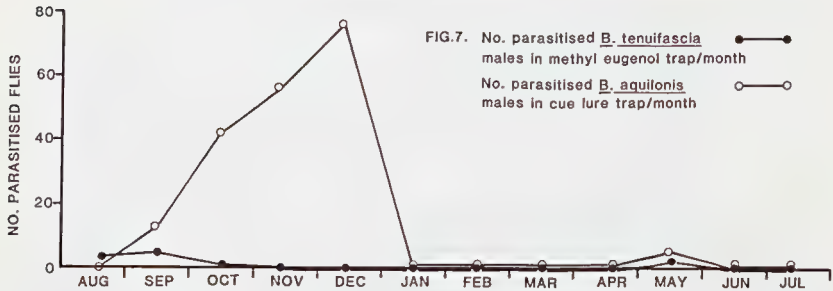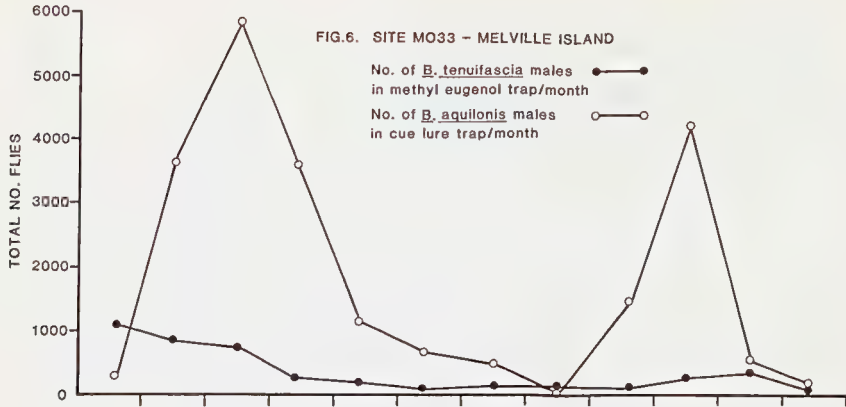
Fig. 5. Percent of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month parasitised by *Dipterophagus daci* at site M007 on Melville Island.

Materials and Methods

The work was carried out in a region across the north of the Northern Territory. Two sites were selected on Melville Island and three on the mainland (Fig. 1). Taracumbi Falls (Site M033) and the site 7 km N of Paru Village are both wet habitats on Melville Island, about 40 km apart. The site at Moline Rock Falls (Site MRF) *ca* 70 km NE of Pine Creek is a wet habitat. The site near the Wildman River (West Branch) *ca* 100 km E of Darwin (Site AH014) and that *ca* 70 km NE of Pine Creek (Site DR004) are classed as dry habitats. The wet sites are characterised by the presence of surface water for the whole year and situated in or near monsoonal rainforest. The dry sites are devoid of surface water for part of the year and are situated in open eucalypt woodland.

The climate of the study area is classified as semi-arid tropical (Williams *et al.* 1985). It is characterised by having a distinct "wet" season during December to April and a "dry" season for the remainder of the year. Mean daily maximum and minimum temperatures, mean relative humidities at 9 am and monthly rainfall data were obtained from weather stations at Garden Point (Melville Island), Middle Point and Pine Creek, selected because of their proximity to the trapping locations (Fig. 2).

Fruit fly populations were monitored at *ca* 100 localities representative of the endemic vegetation. This was part of a broad surveillance strategy for exotic fruit flies carried out under the auspices of the North Australian Quarantine Survey. At each locality two Steiner type fruit fly traps were set, one

Figs. 6 and 7. (6). Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month at site M033 on Melville Island; (7). Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month parasitised by *Dipterophagus daci* at site M033 on Melville Island.

containing methyl eugenol (4 ml + 2 ml 50% w/v malathion e. c.), the other containing cue lure (4 ml + 2 ml 50% w/v malathion e. c.). This study was carried out for one year from August 1977. All traps were cleared of flies at *ca* one-month intervals at which time the lure plus insecticide baits were changed. The trapped flies (all males) were identified, counted and examined under a stereo microscope for presence of strepsipteran parasites. At five localities, selected as wet or dry habitats, the number and percentage of parasitised flies were calculated for two species, *Bactrocera aquilonis* (May) and *B. tenuifascia* (May).

Results

Seasonal abundance

Data are presented for *B. aquilonis* from three sites (M007, M033, AH014) and for *B. tenuifascia* from five sites (M007, M033, MRF, DR004, AH014). At each site flies were present for the entire one year trapping period. Data
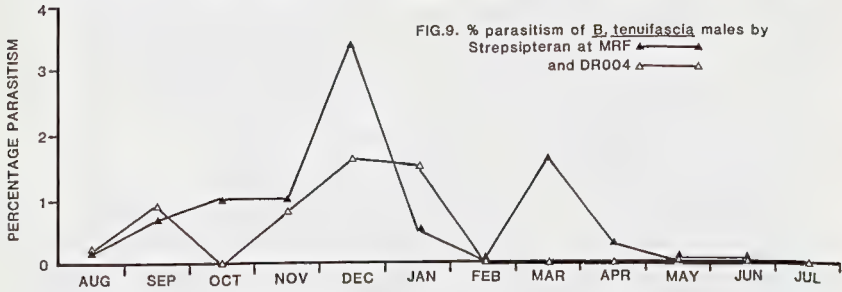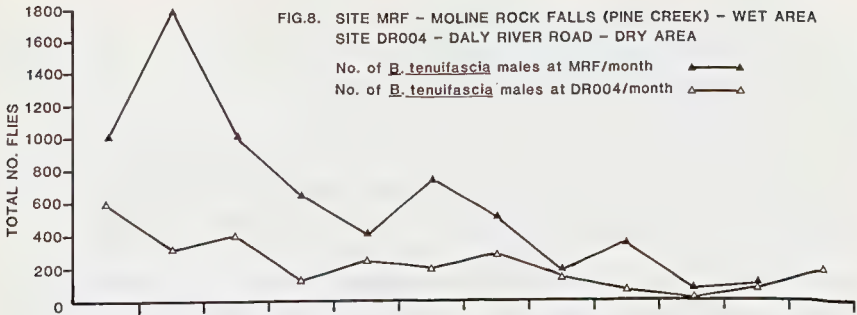
Figs. 8 and 9.   (8). Number of male *Bactrocera tenuifascia* per trap month at sites MRF and DR004 in the Northern Territory; (9). Percent of male *Bactrocera tenuifascia* per trap month parasitised by *Dipterophagus daci* at sites MRF and DR004 in the Northern Territory.

for *B. aquilonis* from MRF and DR004 have not been presented but support conclusions drawn from the other data.

At site M007 the numbers of *B. aquilonis* increased from August to reach a peak (*ca* 6000 trapped flies per month) in mid-October and early November, then declined to mid-January after which they remained at a low level (Fig. 3). At site M033 *B. aquilonis* had two population peaks, in mid-October (*ca* 6000) and mid-May (*ca* 4000), the latter being for a shorter period (Fig. 6). The fruit fly population at M033 showed similar rates of increase and decline in mid-October to that at M007. At site AH014 *B. aquilonis* also had two peaks, one in mid-November and the other in mid-May (each *ca* 1500).

At site M007 the numbers of *B. tenuifascia* increased from mid-September to reach a peak (*ca* 4000) in early December, then declined to mid-March after which they remained at a low level (Fig. 3). At site M033 the numbers of *B. tenuifascia* were low, with a maximum of 1100 in mid-August before declining to *ca* 100 in mid-November, after which they remained at approximately the same level for the remainder of the study period (Fig. 6). At site MRF the numbers of *B. tenuifascia* increased from August to reach a

peak (*ca* 1800) in mid-September, then entered a slow decline to June (Fig. 8). At sites DR004 (Fig. 8) and AH014 (Fig. 10) *B. tenuifascia* reached peaks in mid-August (*ca* 600 and 4000 respectively), after which they entered a slow decline.

Flies parasitised by *D. daci* generally were restricted to shorter periods of the year. At site M007 the number of parasitised *B. aquilonis* increased in mid-September to reach a peak (*ca* 165) in mid-November, then declined to mid-February (Fig. 4). Parasites were present for *ca* 10 months. At the peak of activity of *B. aquilonis* (October-November), the level of parasitism was 2.6% and this reached a peak of 7% in mid-January when the fly population had declined (Fig. 5). Concurrently, the number of parasitised *B. tenuifascia* increased slowly from mid-October to reach a peak in mid-February (*ca* 15), then declined to mid-March (Fig. 4). Parasites were present for 5 months. At the peak of activity of *B. tenuifascia* (early December), the level of parasitism was 0.25% and this peaked at 6.5% in mid-April when the fly population had declined markedly (Fig. 5).

At site M033 the number of parasitised *B. aquilonis* increased from mid-August to peak at mid-December (*ca* 80 flies and 7% parasitism) (Fig. 7). During the second peak of *B. aquilonis* in mid-May there was almost no parasite activity (*ca* 0.1% parasitism) (Fig. 7). At this site the number of parasitised *B. tenuifascia* was at a very low level but followed the population trend of the host species (Fig. 7).

At site MRF the level of parasitism in *B. tenuifascia* was 0.7% at the peak of the fly population, increasing to *ca* 3.5% in mid-December when the fly numbers had declined to a low level (Fig. 9). At site DR004 the level of parasitism in *B. tenuifascia* was *ca* 0.25% at the peak of the fly population, increasing to *ca* 1.5% in mid-December when the fly population was well into its decline (Fig. 9).

At site AH014 the number of parasitised *B. aquilonis* reached a peak in mid-November (Fig. 11). The level of parasitism was *ca* 0.8% during the peak of the fly population in mid-November and 1.3% in December when the host population was low. There was no parasite activity for eight months from mid-January (Fig. 11). At this site the period of parasite activity in *B. tenuifascia* was only four months, from mid-August to mid-December (Fig. 11). The level of parasitism in this fly species was *ca* 0.15% at the peak of its population in mid-August and 0.4% in mid-November when the fly population had declined.

Geographic distribution
D. daci is known in Australia from Melville Island, coastal and subcoastal areas of both the Northern Territory and Cape York Peninsula, some Torres Strait islands and Townsville (northern Qld), Mt Glorious, Palmwoods and
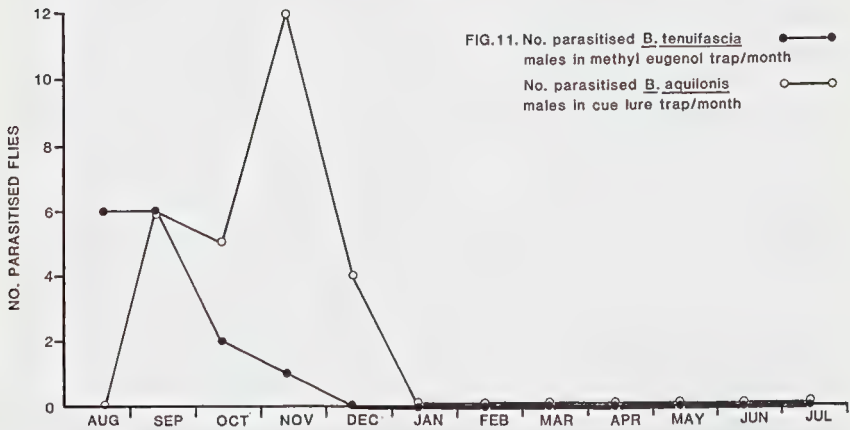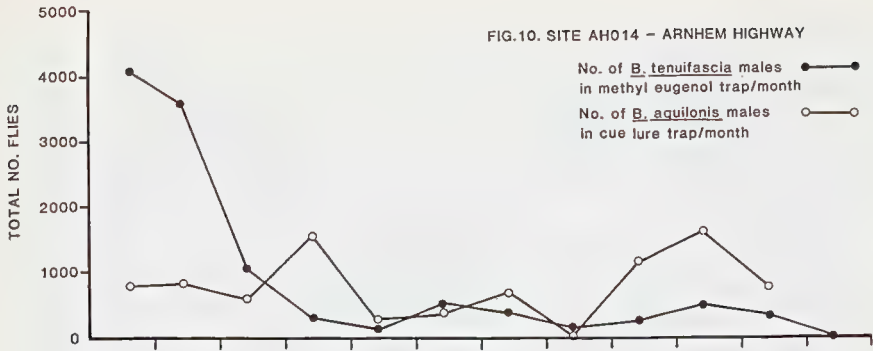
Figs. 10-11. (10). Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month at site AH014 in the Northern Territory; (11) Number of male *Bactrocera aquilonis* and *B. tenuifascia* per trap month parasitised by *Dipterophagus daci* at site AH014 in the Northern Territory.

Redland Bay (SE Qld) (Drew and Allwood 1985, Drew unpublished data). It occurs also on Guadalcanal, Solomon Islands (new record).

Host records
D. daci has been recorded from 19 dacine hosts: *Bactrocera aquilonis* (May), *B. cacuminata* (Hering), *B. decurtans* (May), *B. mayi* (Hardy), *B. neohumeralis* (Hardy), *B. peninsularis* (Drew & Hancock), *B. tenuifascia* (May), *B. tryoni* (Froggatt), *Dacus bellulus* Drew & Hancock (Drew and Allwood 1985), plus *B. abscondita* (Drew & Hancock), *B. aeroginosa* (Drew & Hancock), *B. breviaculeus* (Hardy), *B. frauenfeldi* (Schiner), *B. jarvisi* (Tryon), *B. musae* (Tryon), *B. perkinsi* (Drew & Hancock), *Dacus aequalis* Coquillett (new records from Australia), *B. froggatti* (Bezzi) and *B. umbrosa* (Fabricius) (new records from Solomon Islands). *B. aquilonis, B. musae, B. neohumeralis* and *B. tryoni* are major pest species in Australia.

Discussion

The seasonal activity of dacine fruit flies is dependent upon temperature, rainfall and the state of development of the host fruit (Bateman 1968, Drew and Hooper 1983). Drew and Hooper (1983) also demonstrated that male lure trap catches provided an accurate assessment of the seasonal changes in dacine populations.

Both *B. aquilonis* and *B. tenuifascia* were trapped throughout the year at all sites but their populations increased in the August-December period prior to the onset of the wet season. This was probably due to increasing temperature and relative humidity and increased wild host fruit production, as found for *B. cacuminata* (Hering) by Drew and Hooper (1983). The major wild host fruits of *B. aquilonis* are *Glycosmis trifoliata* (Blume) Sprengel, *Micromelum minutum* (Forster f.) Wight and Arn. and various species of *Syzygium* (Smith *et al* 1988). Their peak fruiting period is October-November, immediately prior to the onset of the wet season. Second peaks in populations of *B. aquilonis* occured from March-May at sites M033 and AH014, coinciding with the fruiting period of *Terminalia ferdinandiana* Exell (March-June). Populations of *B. tenuifascia* also reflected the availability of its major hosts; *Planchonella pohlmaniana* (F. Muell.) fruits April-November while *P. arnhemica* (F. Muell.) P. Royen fruits June-November (Fitt 1981).

Rainfall is probably more important later because of its influence on the survival of pupae and emerging adults (Bateman 1972). The populations of *B. aquilonis* were higher than those of *B. tenuifascia* at all study sites. Populations of *B. aquilonis* were 3-4 times larger in the wet habitats (M007 and M033) than in the dry habitat (AH014). Similarly, populations of *B. tenuifascia* were usually higher in the wet habitats but this difference was not as consistent as in *B. aquilonis*.

The increase in parasite activity followed that of the host flies. However, there was a one month lag period for the parasite in *B. aquilonis* and a two month lag period in *B. tenuifascia*. The activity of the parasites coincided with the onset of the wet season and even when there was a second *B. aquilonis* population peak at M033, in the dry season, the parasites were virtually absent. There was a shorter period of parasite activity and a lower % peak parasitism level in both host species in the dry habitats. The level of parasitism in *B. tenuifascia* was consistently lower than that in *B. aquilonis*, indicating that the latter species is a better host for the parasite.

The seasonal activity of *D. daci* was dependent upon the availability of its hosts and rainfall. However, in spite of the availability of large fruit fly populations, the parasite was not efficient in inducing high rates of parasitism. There were very low percentages of parasitism when the fly populations were at their peaks and higher levels only when the fly populations declined markedly. This may be explained by the fact that *Bactrocera* species are *r* selected species, undergoing rapid increases in

population when host fruits are available and environmental conditions permit (Bateman 1972, Drew and Hooper 1983). The rapid population increases of the host species appear too large for the rate of increase of the parasite. Although no evidence exists, low levels of parasitism by *D. daci* may be explained by low survival rates of triungulins, small numbers of triungulins actually coming in contact with fruit fly adults, or male dacines being less favoured as hosts than females.

There was no apparent effect on the external appearance of the host and on the size and colour of the testes, similar to *Corioxenos antestiae* Blair parasitising *Antestia* spp. (Pentatomidae) in Africa (Kirkpatrick 1937). However, in *Antestia* the stylopised females never produced mature eggs and the stylopised males were incapable of fertilising eggs even when they copulated. Even if *D. daci* has a similar effect on its fruit fly host species, it seems that it will never have a marked influence on population reduction. Kirkpatrick (1937) suggested that the combination of an egg parasite and a strepsipteran may have a better chance of inducing larger population reductions in *Antestia.*

Gregarious parasitism, recorded by Drew and Allwood (1985), occurs with larger numbers of parasites per host than that reported by Kirkpatrick (1937). We have observed the fungus infection in the empty male pupal cases recorded by Kirkpatrick (1937) and Bohart (1941). One female parasite collected at Palmwoods, SE Qld, had over 3000 triungulin larvae indicating that they have a very large reproductive rate. This is probably essential as the triungulins must be exposed to severe environmental stresses between emerging from the female and finding a host.

Dipterophagus daci has now been recorded in 19 dacine host species and more frequently in Cape York Peninsula than SE Queensland. There is no evidence to suggest that it is going through a southward expansion of its distribution. It predominates in the northern tropics and it is probable that recordings in SE Qld are related to increased collections of flies for other ecological studies and bait spray trials.

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